CRUSTACEAN CHEMICAL PERCEPTION: TOWARDS A THEORY ON OPTIMAL CHEMORECEPTION

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ABSTRACT

Experiments explored how crustacea respond to odors that could signal energy and nutrient properties of food. While free amino acids are abundant in living prey, they diffuse rapidly from carrion and are assimilated by biodegradatory bacteria concomitant with release of ammonia. The ratio of amino acids to ammonia decreases with increasing carrion age and is proposed to signal the relative nutritional (nitrogen) quality of food. Supporting this hypothesis are data showing six bathypelagic and littoral species probing and searching to amino acids, but not to ammonia. Amino acids caused forward ambulation (searching) in some species while ammonia induced only tail-flipping (fleeing) in others. Interactions between amino acids and ammonia were clearly antagonistic, since mixtures combining these substances suppressed both feeding and fleeing. Additional experiments with the spiny lobster, *Panulirus interruptus,* demonstrate that excitation by the high energy molecule, ATP > ADP > AMP = adenosine, which is the pathway followed in autolytic degradation of animal flesh. Solutions identical in ATP evoked searching and feeding according to their ranked order of adenylate energy charge. Results indicate that crustacea respond best to odors that may specify food of highest energy and nutrient content, though responses differ between species and probably reflect differences in dietary habits.

INTRODUCTION

A major problem for animals is how to exploit food resources efficiently. Ability to remotely sense food quality, quantity, and effort needed for food capture is clearly advantageous. This minimizes time choosing food and maximizes net rate of energy or nutrient gain (Hughes, 1979; Erichsen *et al.,* 1980; Orians, 1981). The decision to feed is based on many factors, including internal motivational states (level of starvation, social dominance, sex, and reproductive status; McFarland, 1971; Dethier, 1976; Harrison, 1983; Tilson and Hamilton, 1984; Bell *et al.,* 1985) and external environmental qualities, such as presence of predators or competitors (Milinski and Heller, 1978; Nelson and Vance, 1979; Barnard and Brown, 1981; Kacelnik *et al.,* 1981; Lima, 1985a; Schmitt and Holbrook, 1985). Foragers are influenced by stimuli specific to food, especially by smell and taste, which are vital to ingestion (Linstedt, 1971; Dethier, 1976; Ache, 1982; Croll, 1983, among others) and to activating and orienting search (Bell and Tobin, 1982). Chemical senses evolve to increase efficiency of resource use, given the goal of a forager is to minimize time spent acquiring set reward or is to maximize net rate of energy or nutrient gain.

Models of optimal foraging usually assume that grazers have complete prior knowledge of resource distributions, or that such knowledge is gained by cost-effective sampling. An implicit assumption is that foragers must distinguish the compara-

tive worth of prey, usually by some unspecified mechanism in order to make the "right" energetic decision when grazing in a mixed prey assemblage. How sampling proceeds is poorly understood (but see Krebs *et al.,* 1978; Lima, 1985b), especially with regard to sensory mechanisms and perceptual ability.

This investigation determined how crustacea perceive chemicals that could specify energy and nutrient qualities of food. Marine crustacea were used because they depend almost exclusively on chemoreception in feeding (Hazlett, 1968; Schembri, 1982; Zimmer-Faust and Case, 1982a) and their behavior is highly stereotyped and easily quantified (Fuzessery and Childress, 1975; Field, 1977; Pearson *et al.,* 1979; Zimmer-Faust and Case, 1982b). Crustacea respond to a wide range of low molecular weight compounds that are readily synthesized (McLeese, 1970; Shelton and Mackie, 1971; Mackie, 1973; Carr, 1978; Robertson *et al.,* 1981; Zimmer-Faust *et al.,* 1984b), which makes them highly useful in chemical senses research.

A verbal model

Free amino acids are abundant as osmolytes in tissues of all living aquatic invertebrates, the principal dietary items of crustacean omnivores (Clark, 1968; Gerard and Gilles, 1972; Clark and Zounes, 1977; Bowlus and Somero, 1979; Zurburg and De-Zwaan, 1981; Yancey *et al.,* 1982). Because amino acids diffuse rapidly from carrion once a prey dies (Rittschof, 1980; Zimmer-Faust and Case, 1982a), they probably specify living or freshly killed prey. Free amino acids can be used as a source of nitrogen for protein synthesis and comprise as much as 8–10% of the dry weight of invertebrate flesh. Ammonia, on the other hand, is a nitrogenous waste product of transamination in protein catabolism and non-nutritive to crustacea (Campbell, 1973). Biodegradatory bacteria selectively assimilate other low molecular weight compounds, including amino acids (Ogura, 1975), while they produce copious amounts of ammonia (Hollibaugh, 1979; Kjosbakken *et al.,* 1983). The ratio of amino acids to ammonia decreases with increasing carrion age and decomposition (Kjosbakken *et al.,* 1983; Michel and Zimmer-Faust, unpubl. data); consequently, a corresponding reduction in predatory feeding might be expected. Interactions between amino acids and ammonia are proposed to signal the relative nutritional (nitrogen) quality of food.

Adenosine 5'-triphosphate (ATP) is involved either directly or indirectly with all cellular chemical energy transfers (Atkinson, 1977). Because ATP decays rapidly during cell death (Hiltz and Dyer, 1970), it is commonly used by ecologists to estimate "living" biomass (Holm-Hansen and Booth, 1966; Sinclair *et al.,* 1979; Ward and Cummins, 1979). Predator sensitivity to ATP alone cannot provide a reliable energy measure; cellular concentrations vary greatly depending on organismal life history stage, activity level, and on long-term seasonal factors (Bamstedt and Skjoldal, 1976; Sjkoldal and Bamstedt, 1976; Giesy and Dickson, 1981). Adenylate energy charge [AEC = (ATP + 0.5 ADP)/(ATP + ADP + AMP)] is a ratio of high energy phosphate bonds expressed as a function of the total phosphoadenylate pool. AEC scales from 0 to 1, with 1 indicating pure ATP (two high energy phosphate bonds) and 0 indicating pure AMP (zero high energy phosphate bonds). In normal healthy organisms (from bacteria to rats), an AEC of 0.8–0.9 is maintained even at the expense of compromising stored energy reserves. Ratios fall to ≤ 0.5 in dead, diseased, or in highly stressed organisms, only after energy reserves have been depleted (Chapman *et al.,* 1971; Balch, 1972; Ridge, 1972; Walker-Simmons and Atkinson, 1977; Ostolovskii, 1978; Buikema, *et al.* 1979; Ivanovici, 1980; Karl, 1980). Because AEC is indicative of the total metabolic energy available to an organism (Atkinson, 1977), its perception by a predator might assist in recognizing prey energetic quality. Predator sensitivity to ATP, as well as to AEC, was therefore expected.
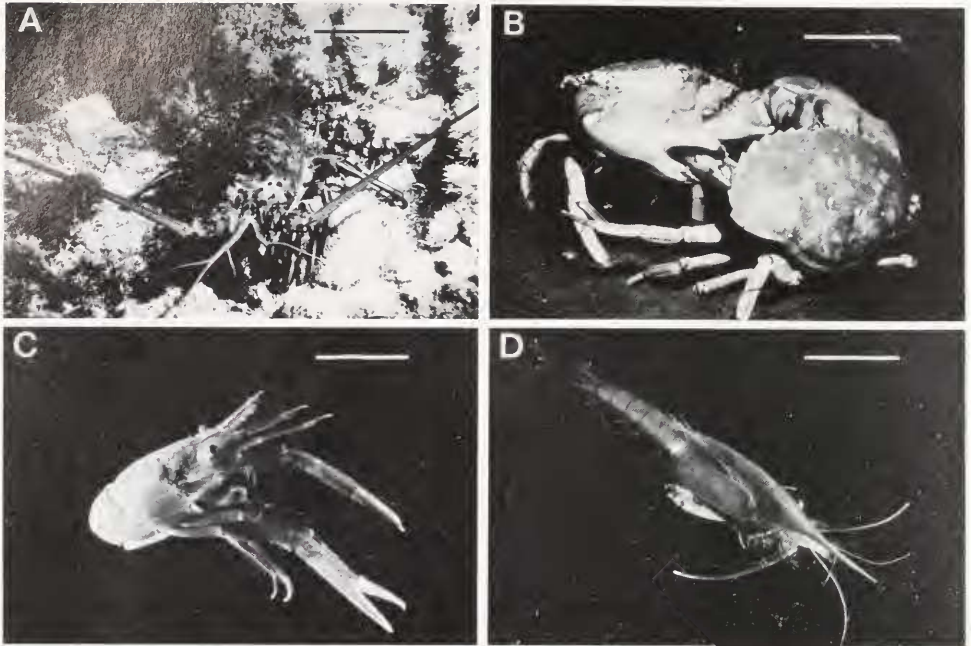
FIGURE 1. Animals representing four of six tested species, showing differences in morphologies and habitats. A. Spiny lobster, *Panulirus interruptus;* scale bar = 6 cm. B. Yellow crab, *Cancer anthonyi* (two individuals appear); scale bar = 6 cm. C. Pelagic red crab, *Pleuroncodes planipes;* scale bar = 2 cm. D. Deep sea mysid, *Gnathophausia ingens;* scale bar = 2 cm. Not shown are the hermit crab, *Pagurus hirsuti-usculus,* and the majid crab, *Podochela hemiphilla.*

MATERIALS AND METHODS

Species chosen for investigation presented a broad range of dietary preferences and habitats (Fig. 1 and Table I). Following collection, animals were held in 3000 l aquaria with flowing seawater at ambient temperature (15–17°C). A 12:12 D:L cycle (light on:0700 h) was imposed for two weeks. Animals were fed *ad libitum* on mackerel (*Scomber japonicus*) and salmon muscle (*Oncorhynchus* spp.), then food was withheld for 24 h prior to testing. Chemical solutions were presented to animals placed in plexiglas aquaria (30 × 30 × 15 cm), constructed to allow precise control of stimulus flow characteristics without inhibiting behavior (Zimmer-Faust and Case, 1983). A primary seawater flow (980 ml/min) entered each aquarium from a head-tank maintained under constant hydrostatic pressure, while a secondary flow (120 ml/min) served to inject test substances (10 ml/7 s). Dilution associated with injection of a fluorescent dye was 1.02×10^{-3} ($\pm 0.13 \times 10^{-3}$ SD) times the original concentration, as measured at the olfactory appendages (antennules) of test animals (see methods of Zimmer-Faust and Case, 1983). Presently reported concentrations are uncorrected for this dilution.

Test procedures were modified slightly for assays with *Gnathophausia,* since this animal required holding at an ambient temperature of 5°C. Individuals were maintained in 1-liter plastic containers and positioned in a constant temperature room (5°C), with seawater changed weekly. *G. ingens* has been maintained for up to 2.5 years under these conditions (Childress and Price, 1978). Test solutions (2 ml/10 s) were added directly to containers and seawater was changed following each trial.

TABLE I

Collection histories of tested animals

Order Infraorder Genus species	Habitat	Depth (m)	Size (mm) ($\bar{x} \pm$ SD)	Principal dietary components
Decapoda				
Palinura				
Panulirus interruptus	Rock reef	3–7	67.4 ± 4.0[a]	Animal flesh
Brachyura				
Cancer anthonyi	Sand flat	25–40	142.2 ± 8.4[b]	Animal flesh
Podochela hemiphilla	Pier piling	2–5	13.8 ± 2.0[a]	Algae, animal flesh
Anomura				
Pagurus hirsutiusculus	Rock intertidal	0	5.8 ± 0.8[a]	Detritus, animal carrion
Pleuroncodes planipes	Midwater	100–200	30.1 ± 2.6[a]	Animal flesh, zooplankton
Mysidacea				
Lophogastrida				
Gnathophausia ingens	Midwater	400–600	32.4 ± 3.4[a]	Animal flesh, zooplankton

[a] Measured as carapace length.
[b] Measured as carapace width.

Experimental procedures

These were nearly identical to those previously described (Zimmer-Faust *et al.*, 1984b). Animals were tested a maximum of 4 times during a 14-day period, but only once each 72 h. They were put into experimental aquaria 30–60 min prior to testing and observed for 1 min before and for 4 min after chemical presentation. Trial length was chosen to maximize differences in responses to test and control stimuli, as determined in preliminary experiments. All tests were conducted using a double-blind protocol in which the observer was unaware of the composition of solutions introduced. Order of chemical presentation was established using a random numbers table with the exception that identical solutions were never repetitively introduced to the same animal. Solutions were prepared immediately before testing using analytical grade reagents and 0.45 μm filtered seawater, adjusted to pH 7.8.

Preliminary experiments evaluated responses to the amino acids, taurine, glycine, and glutamic acid. These were selected because of their proven ability to maximally excite crustacean feeding (McLeese, 1970; Fuzessery and Childress, 1975; Ache, 1982; Zimmer-Faust *et al.*, 1984b). Glycine was found most stimulatory to *Panulirus, Cancer, Pleuroncodes,* and *Gnathophausia,* while glutamic acid was most stimulatory to *Pagurus* and *Podochela.* These compounds were used as stimuli in the following tests.

Responses to amino acids and to ammonia

Solutions of 10^{-2} M amino acid, 10^{-2} M ammonia, 10^{-2} M amino acid plus 10^{-2} M ammonia, and seawater, were presented to 24 specimens of each species. The injected concentration ($=10^{-2}$ M) produced a dilution-corrected 10^{-5} M in contact with the animals. This was appropriate given background levels of glycine and glutamic acid of 3×10^{-8}–3×10^{-7} M, and ammonia of 8×10^{-7}–3×10^{-6} M, in aquaria seawater with animals present (see Manahan *et al.*, 1983, for chemical analytical methods). Free amino acids are individually maintained at 10^{-4}–10^{-6} moles/g (dry

weight), and ammonia at 10^{-6} moles/g, in the flesh of invertebrate prey consumed by crustacea (Clark and Hinkle, 1981; Zurburg and DeZwaan, 1981). Additional tests with *Panulirus* and *Pleuroncodes* investigated effects of ammonia concentration on amino acid responses. Solutions of 10^{-5}, 10^{-4}, 10^{-3}, and 10^{-2} M ammonia were presented alone, and with 10^{-2} M glycine. Twenty animals from each species were tested with solutions. *Panulirus* was also tested with a mixture of 11 amino acids comprising >95% of the total free amino acid pool in abalone muscle, a preferred food (Zimmer-Faust *et al.,* 1984a). This was presented with, and without, 10^{-2} M ammonia added (n = 20 animals).

Responses to adenylates

The spiny lobster, *Panulirus,* was further assayed for responses to ATP, ADP, AMP, and adenosine (ADO) at 10^{-4}, 10^{-3}, and 10^{-2} M. Tests were limited to lobsters because of time constraints and because adequate numbers of specimens were lacking for bathypelagic species. Twenty lobsters were tested with each solution. Subsequent trials employed a factorial design to present ATP, ADP, and AMP in all combinations. Each substance was maintained at 10^{-2} M. It was determined whether lobsters are best stimulated by the mixture of highest adenylate energy charge; by the mixture of highest total phosphoadenylate concentration; or by ATP (alone) independently of other phosphoadenylates. The injected concentration of 10^{-2} M produced a dilution-corrected 10^{-5} M in contact with animals. Individual phosphoadenylates are maintained at 10^{-4}–10^{-6} moles/g (dry weight) in the flesh of invertebrate prey consumed by crustacea (Hiltz and Dyer, 1970; Ansell, 1977).

Experiments with large tanks

The above experiments poorly simulated natural conditions. This was especially true for *Panulirus* and *Cancer;* these animals were large relative to the size of test-aquaria. For this reason, several assays were repeated with isolated *Panulirus* and *Cancer* in large outdoor arenas (1.5 m diameter $\times$ 0.6 m water depth), with sandy substrates, shelters, and continuous flowing seawater (8 l/min). Experiments were performed at night under ambient moonlight (intensities = 0.02–0.06 $\mu W/cm^2$) with animals placed in arenas 24 h prior. Each animal was tested only once with a solution of 10^{-5} M glycine, 10^{-5} M ammonia, 10^{-5} M glycine plus 10^{-5} M ammonia, 10^{-5} M ATP, or seawater. These were pumped to the olfactory region (antennules) at 30 ml/ 180 s, through polyethylene tubing (0.32 cm ID) threaded in a hand-held acrylic rod. Sterile cotton was affixed at the tip to diffuse chemicals and to reduce mechanical disturbances caused by stimulus applications. Behavior was observed with an image intensifier and a 75 mm night vision lens (Javelin Electronics Model 221). A positive response was scored when an animal turned, walked towards, then attempted to grasp the cotton tip during a chemical presentation.

Addressing the question of mixture interaction

Probability of response to a chemical presentation, $p(i + j)$, was a function of chemical [$p(i)$] and non-chemical [$p(j)$] factors (*e.g.,* spontaneous activity). Although $p(i)$ and $p(j)$ were assumed independent and binomially distributed, their distributions were not necessarily disjoint; consequently, $p(i)$ could not be directly measured. I used responses to seawater (control) in estimating $p(j)$ and determined $p(i)$, as follows:

$$p(i + j) = p(i \cup j) = p(i) + p(j) - p(i \cap j) \tag{1}$$

Because i and j were independent, $p(i \cap j) = p(i)p(j)$, and $p(i)$ was solved algebraically:

$$p(i + j) = p(i) + p(j) - p(i)p(j)$$

and,

$$p(i + j) = p(j) + p(i)[1 - p(j)]$$

so,

$$p(i) = \frac{p(i + j) - p(j)}{1 - p(j)} \tag{2}$$

Binary mixture interaction between any two chemical agents, a and b, was evaluated by assuming that chemical effects were independent and additive. These assumptions were identical to those made by previous investigators who used "response addition" models to predict responses to mixtures (*sensu* Hyman and Frank, 1980). In this study the expected probability of response to a mixture, $p(i)_{a+b}$, was modelled by the equation,

$$p(i)_{a+b} = p(i)_a + p(i)_b - [p(i)_a p(i)_b] \tag{3}$$

An independent component index, $f(R)$, was thus derived as:

$$f(R) = p(i)_{a+b} - \{p(i)_a + p(i)_b - [p(i)_a p(i)_b]\} \tag{4}$$

where $p(i)_{a+b}$, $p(i)_a$ and $p(i)_b$ were determined empirically. Independence between chemical effects was achieved at $f(R) = 0$, and $p(i)_{a+b} = p(i)_a + p(i)_b - [p(i)_a p(i)_b]$. Limits were established at $-1 \leq f(R) \leq 1$, given $0 \leq p(i) \leq 1$. Response synergy occurred from 0 to 1; suppression from 0 to -1; additivity occurred at zero. This index was similar to that of Hyman and Frank (1980), but with improvements made to account for the binomial nature of present data and to give equal weight to response synergy and suppression.

RESULTS

Behavioral sequences defining early searching and appetitive phases of feeding are given in Table II, with descriptions taken from previous investigators wherever possible. For this study, it was necessary to derive behavioral sequences only for *Podochela* by watching animals before and after food presentations (= algal turf). I chose cheliped flexion (where applicable) or contact between antennules and mouthparts as criteria for "feeding," since these are exhibited stereotypically by crustacea (Mackie and Shelton, 1972; Snow, 1973; Fuzessery and Childress, 1975; Field, 1977; Pearson *et al.*, 1979; Zimmer-Faust and Case, 1982b; Trott and Robertson, 1984; Zimmer-Faust *et al.*, 1984a, b) and are of obvious utility either in contacting food, or in maintaining chemoreceptors functioning in orientation to food odor (Hazlett, 1968, 1971; Reeder and Ache, 1980; Devine and Atema, 1982). For *Gnathophausia,* I assayed alternating flexion and extension of endopodites on the maxillipeds as an appropriate indicator of feeding (Fuzessery and Childress, 1975). Locomotory behavior was monitored as movement of ≥ 1 carapace length, either forwards or backwards.

Responses to amino acids and to ammonia

Applications of amino acids, but not of ammonia, caused significant feeding responses relative to seawater (Fig. 2; G-Test for Independence with Williams' correction: $G \geq 10.49$, d.f. = 1, $P < 0.005$, comparisons for all six species). Independent component indices were all negative for mixture interactions (Fig. 3), and amino

Sequential behavioral patterns in appetitive phases of feeding

Animal	Behavioral sequences
Panulirus interruptus[a]	(1) Antennule flicking rate is increased. (2) Pereiopods are extended and/or used to prod the substratum. (3) The third maxillipeds are flared and set into a lateral motion. (4*) Antennules are vertically deflected and brought into contact with the mouthparts.
Cancer anthonyi[b]	(1) Antennule flicking rate is increased. (2) Pereiopods are extended and/or used to prod the substratum. (3) The third maxillipeds are flared and set into a lateral motion. (4) Antennules are vertically deflected and brought into contact with the mouthparts. (5*) Chelipeds are extended and/or used to prod the substratum.
Podochela hemiphilla[c]	(1) Antennule flicking rate is increased. (2) The third maxillipeds are flared and set into a lateral motion. (3*) Chelipeds are extended and/or used to prod the substratum.
Pagurus hirsutiusculus[b]	(1) Antennule flicking rate is increased. (2) The third maxillipeds are flared and set into a lateral motion. (3) Pereiopods are extended and/or used to prod the substratum. (4*) Chelipeds are extended and/or used to prod the substratum, then brought to the mouth.
Pleuroncodes planipes[b]	(1) Antennule flicking rate is increased. (2) The third pair of maxillipeds are rubbed together. (3) The third pair of maxillipeds are outstretched and brought back to the mouth. (4) Pereiopods and chelipeds are extended and/or used to prod the substratum. (5*) Chelipeds are brought back to the mouth.
Gnathophausia ingens[b]	(1) Anterior endopodites are moved in a circular motion over the mouth. This motion appears to be related to filter feeding. (2) Endopodites are partially extended in an unconcerted manner. (3*) Endopodites are extended approximately perpendicular from the body in a concerted motion. (4) The abdomen is arched ventrally, either perpendicular to the body or with the telson almost in contact with the mouth.

Sources of behavioral descriptions: [a]Zimmer-Faust *et al.,* 1984b; [b]Fuzessery and Childress, 1975; [c]present study.

Asterisks (*) denote defining acts.

acid stimulations of feeding were significantly suppressed by ammonia in *Panulirus, Cancer,* and *Podochela* [$p(i)_{a+b} < p(i)_a$, and G-Test for Independence with Williams' correction: $G \geq 4.29$, d.f. $= 1$, $P < 0.05$, all comparisons]. Similar results were obtained for *Panulirus* when the 11-component amino acid mixture was applied. This caused 70% of all tested animals to "feed" and 65% to walk, while only 35% "fed" and 10% walked following addition of ammonia (G-Test for Independence: $G \geq 4.92$, d.f. $= 1$, $P < 0.05$, both comparisons). The number of times a defining behavioral act was performed in each trial provided a measure of response intensity. For *Cancer, Pagurus,* and *Pleuroncodes,* response intensities evoked by amino acids were significantly depressed by ammonia (Table III; Student's two-tailed *t*-test for small sample sizes, variances assumed equal: $P \leq 0.08$, all comparisons). The intensities exhibited by *Panulirus* and *Podochela* were only slightly affected by ammonia ($P > 0.20$).

Littoral species walked forward to amino acids but not to ammonia, while bathypelagic species tail-flipped backward (fleeing) to ammonia but not to amino acids (Fig. 2). Mixtures reduced significantly the initiation of walking by *Panulirus,* and fleeing by *Pleuroncodes* and *Gnathophausia* [Fig. 3; $p(i)_{a+b} < p(i)_a$ and G-Test: $G \geq 4.14$, d.f. $= 1$, $P < 0.05$, for all comparisons]. The amino acids and ammonia acted antagonistically though which stimulated while the other suppressed depended on the behavior in question (walking or fleeing, respectively).
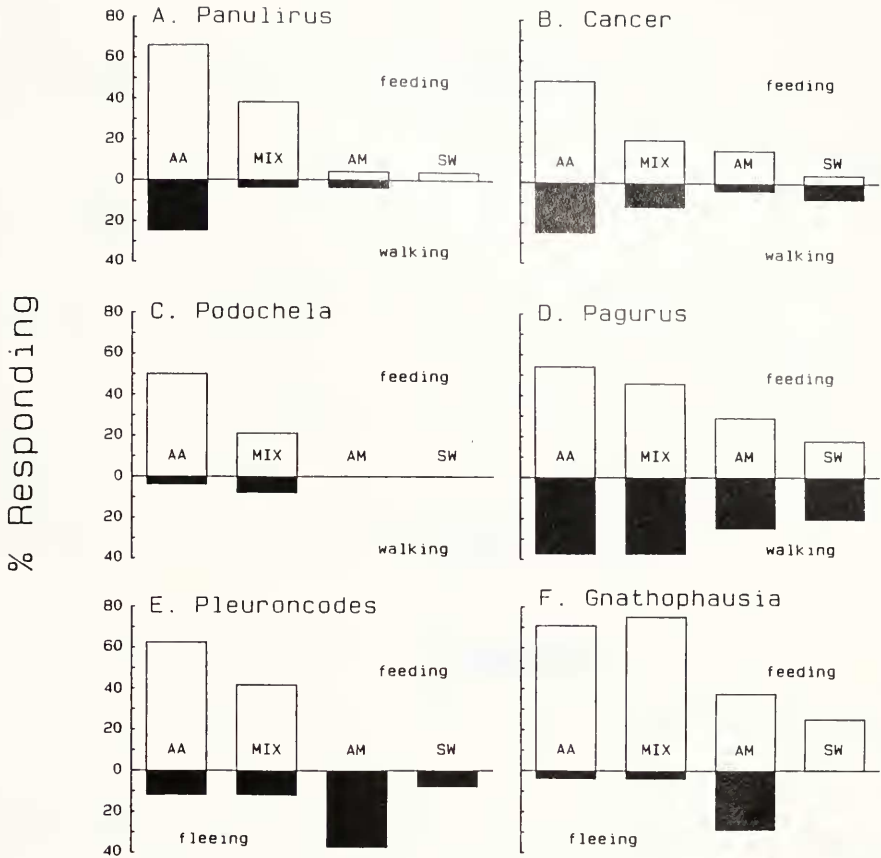
FIGURE 2. Feeding and locomotory responses to amino acid (AA), ammonia (AM), amino acid + ammonia (MIX), and seawater (SW). Each chemical was presented at 10^{-2} M. Forward ambulation (walking) was exhibited only by littoral, and tail-flipping (fleeing) only by bathypelagic species.

Ammonia was slightly inhibitory at 10^{-4} M, and significantly so at 10^{-3} M to glycine-induced feeding by *Panulirus* and chela probing by *Pleuroncodes* (Fig. 4; $P < 0.05$). Ammonia inhibited walking by *Panulirus*, just as it stimulated fleeing by *Pleuroncodes* at the same concentrations ($=10^{-3}$–10^{-4} M) (Fig. 5). Dose-response data show ammonia consistently inhibitory or repellent over a broad range of concentrations.

Responses to adenylates

Adenosine triphosphate was highly stimulatory to *Panulirus* at 10^{-2} M (G-Test: $G \geq 6.50$, d.f. = 1, $P < 0.01$, comparisons for feeding and walking), while ADP was only slightly stimulatory ($P > 0.10$). Both AMP and ADO were without stimulatory effects (Fig. 6). Stimulation by ATP was not independent of the other phosphoadenylates, since differences were nearly significant between the responses to ATP, ATP + ADP, ATP + AMP, and ATP + ADP + AMP (Fig. 7A; G-Test for Independence with Williams' correction: $G = 7.16$, d.f. = 3, $P = 0.06$, for feeding). It was proposed
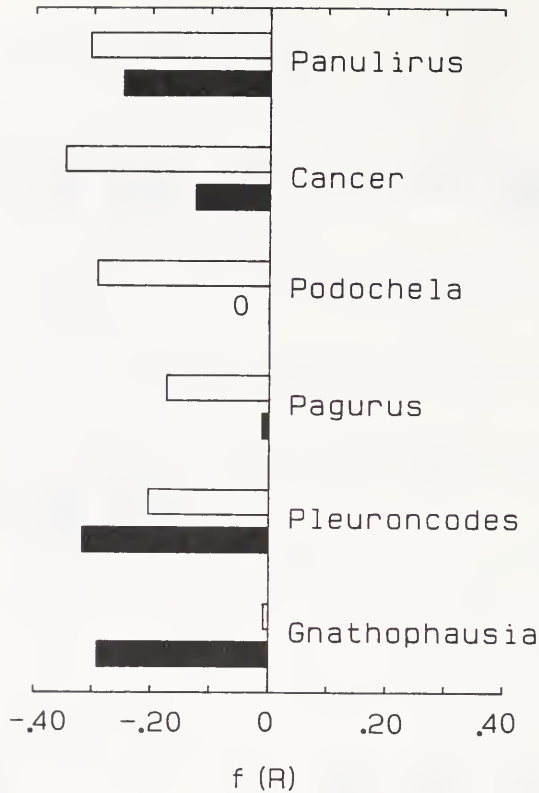
FIGURE 3. Independent component indices for interactions between amino acids and ammonia. Open bar (□), feeding; closed bar (■), locomotion (walking or fleeing). Negative values indicate suppression.

that ADP and AMP might enhance ATP stimulation according to the increase in adenylate concentration. This predicted that proportions of responding animals should be ranked, ATP + ADP + AMP > ATP + ADP = ATP + AMP > ATP. Observed rankings showed no positive association with that predicted (Kendall's one-tailed Tau, with correction for ties: $T \leq -0.40$, n = 4, $P > 0.80$, comparisons for feeding and walking; Accept H_0: no association). It was alternatively postulated that ADP and AMP might inhibit ATP stimulation according to the decrease in adenylate energy charge. This predicted that proportions of responding animals should be ranked, ATP > ATP + ADP > ATP + ADP + AMP = ATP + AMP = ADP > ADP + AMP > AMP. Because the observed rankings correlated positively only with those predicted by this last hypothesis, lobster chemosensitivity to adenylate energy charge is indicated (Kendall's one-tailed Tau, with correction for ties: $T \geq 0.827$, n = 7, $P < 0.02$, comparisons for feeding and walking; Reject H_0: no association, accept H_a: positive association).

Stimulation by ATP was not inhibited significantly by ADP (Fig. 7B; G-Test for Independence with Williams' correction: $G \leq 2.85$, d.f. = 1, $P > 0.10$, both comparisons), though it was by AMP [$p(i)_{a+b} < p(i)_a$, and G-Test: $G = 4.65$, d.f. = 1, $P < 0.05$ for feeding]. The stimulation by ADP was independent of AMP.

TABLE III

Response intensities ($\bar{x} \pm$ SEM) to applied chemical solutions[a]

		Chemical solution			
Animal	Behavior	Amino acid	Amino acid + ammonia	Ammonia	Seawater (control)
Panulirus interruptus	Antennule wiping	8.8 ± 2.0 (n = 17)	11.4 ± 3.5 (n = 10)	—	—
Cancer anthonyi	Cheliped flexion	4.4 ± 0.4 (n = 12)	2.9 ± 0.3 (n = 5)	—	—
Podochela hemiphilla	Cheliped flexion	8.4 ± 2.5 (n = 12)	7.3 ± 3.4 (n = 5)	—	—
Pagurus hirsutiusculus	Cheliped flexion	34.0 ± 5.5 (n = 13)	23.0 ± 4.4 (n = 11)	16.4 ± 7.4 (n = 7)	13.0 ± 1.5 (n = 4)
Pleuroncodes planipes	Cheliped flexion	6.0 ± 0.8 (n = 15)	3.9 ± 0.5 (n = 10)	—	—
Gnathophausia ingens	Endopodite extension	NOT DETERMINED			

[a] Data are the numbers of acts performed in 4 min trials. Values appear only where more than one of 24 tested animals responded. Parentheses denote the number of responding animals.

Experiments with large tanks

Cancer was highly responsive to glycine but less so to the glycine-ammonia mixture (Fig. 8A). An independent component index of −0.240 for this interaction was nearly identical to those of −0.142 and −0.367 calculated from tests using smaller aquaria (Fig. 3). *Panulirus* was also highly responsive to glycine, as well as to ATP (Fig. 8B). The interaction between glycine and ammonia was again inhibitory and produced an index of −0.465, or nearly the same as before (−0.240 and −0.301, see Fig. 3). Experiments with large tanks confirmed the results from tests using smaller aquaria.

DISCUSSION

Although chemosensory responses in this study were products of chemicals applied individually, significant mixture interaction occurred which caused behavioral suppression. Suppression is commonly reported in psychophysical investigations of odor and taste perception (Moskowitz, 1972; Berglund, 1974; Bartoshuk, 1975, 1977; Carefoot, 1982), though present findings go further in proposing an ecological function. Suppression gives control over the modulation and tuning of feeding according to overall perceived quality of a chemical signal. I propose that interactions between chemical agents function, in part, by tuning responses to relative energy and nutrient properties of odor. Mixture suppression might then benefit a searching organism by reducing its response to lower quality foods. Such behavior would be most advantageous under conditions where prey are relatively abundant and food is non-limiting, and where the optimal response is to graze selectively.

It might be argued that suppressant interactions between single amino acids and ammonia are relatively meaningless, given that prey flesh is naturally a complex chemical mixture. However, the single stimulants used in this study were those maximizing feeding and locomotory responses. By using binary mixtures in behavioral assays the complexity of ensuing electrophysiological analysis is greatly reduced when
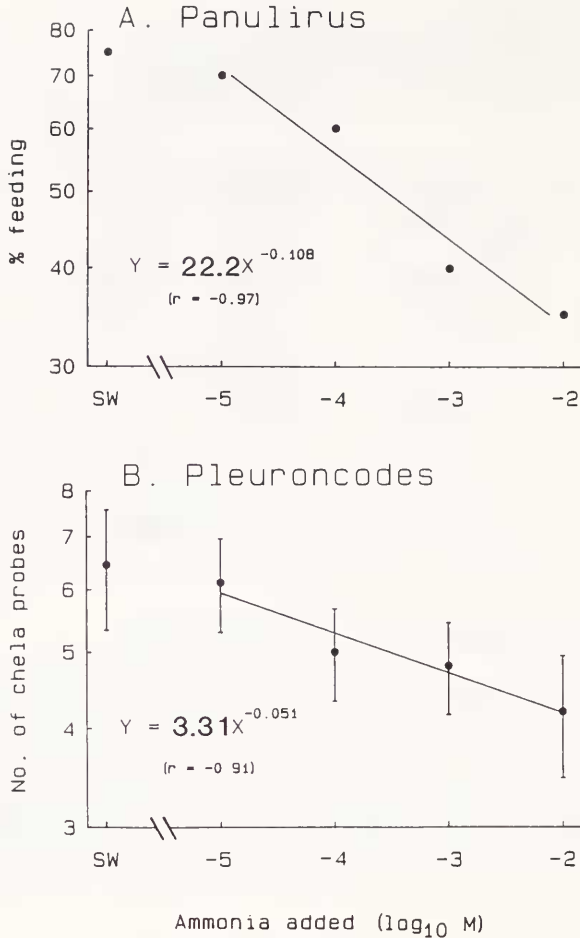
A. Panulirus

$Y = 22.2X^{-0.108}$

$(r = -0.97)$

B. Pleuroncodes

$Y = 3.31X^{-0.051}$

$(r = -0.91)$

Ammonia added $(\log_{10} M)$

FIGURE 4.   Effects of ammonia on 10^{-2} M glycine-induced (A) feeding by *Panulirus,* and (B) cheliped flexion ($\bar{x} \pm$ SD) by *Pleuroncodes.* Responses are adequately modelled as power functions of ammonia concentration. No responses were observed to ammonia presented by itself at 10^{-5}–10^{-2} M. SW: No ammonia added.

considering the neurobiological sites of mixture interaction, *i.e.,* primary receptor or central nervous system. A mixture comprising >95% of the free amino acids in abalone muscle was highly stimulatory to *Panulirus,* but this activity was significantly reduced by the addition of ammonia. Previously, I found a low molecular weight fraction of abalone muscle (<1000 daltons) to be without stimulatory effect to lobsters (Zimmer-Faust *et al.,* 1984a). Experiments later demonstrated that this results from the presence of chemical suppressants, of which ammonia predominates, and not from a lack of stimulatory agents (Zimmer-Faust *et al.,* 1984b).

I interpret results from amino acid and ammonia assays in the following way. Amino acids alone probably trigger attack behavior and intensify within-patch search. Both claw and leg probing were evoked in response to amino acids, and these behaviors are essential to acquiring food in the near-field environment. The amino
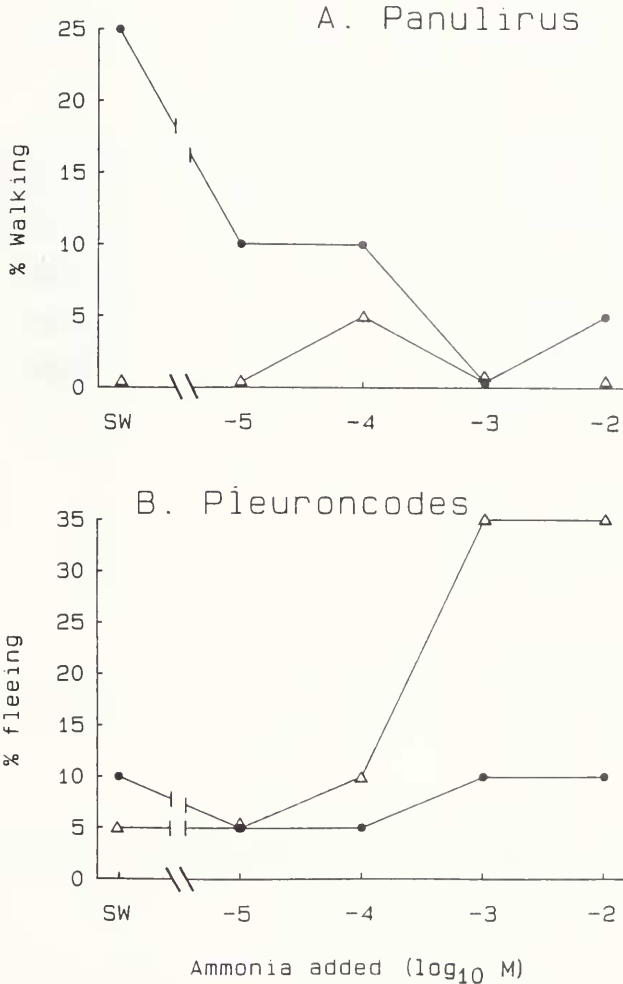
FIGURE 5. Effects of ammonia and glycine on locomotion. A. Walking by *Panulirus* is stimulated by glycine and suppressed by ammonia. B. Fleeing by *Pleuroncodes* is stimulated by ammonia and suppressed by glycine. Closed circles (●) are responses to ammonia with 10^{-2} M glycine added; open triangles (△) are responses to ammonia presented by itself. SW: No ammonia added.

acid induction of walking appeared to possess a klinokinetic or chemotactic compo-nent, since in large tank experiments, *Panulirus* and *Cancer* turned precisely towards a stimulus before moving to grasp the source. Ammonia alone probably causes patch departure. This was demonstrated for bathypelagic species; they tail-flipped away from ammonia. Small tank experiments suggest that littoral species may ignore am-monia, but these experiments did not test animals in an endogenously active state. Large tank experiments confirm that paths of actively moving lobsters (*Panulirus*) and crabs (*Cancer*) are unaltered by ammonia (Zimmer-Faust, unpubl. analyses of video data). Endogenous movements would carry these animals to alternative patches in natural habitats.
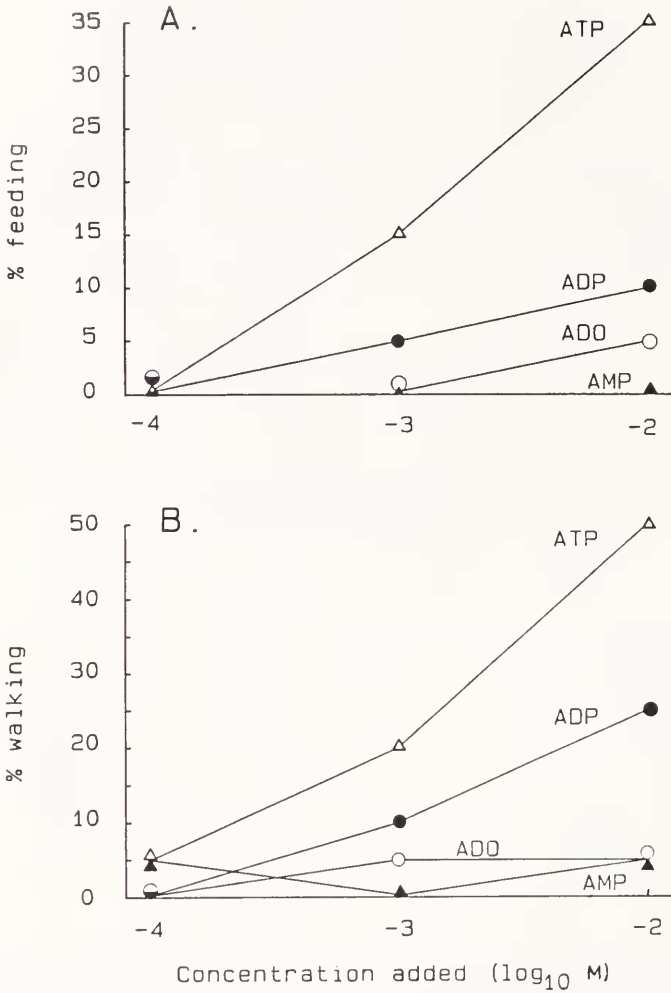
FIGURE 6.   Dose-responses for (A) feeding, and (B) walking by *Panulirus* to the adenylates: ATP, ADP, AMP, and adenosine (ADO).

Mixtures suppressive to the initiation of feeding by *Panulirus* and *Podochela* were not inhibitory to the response intensity. The opposite was true for *Pagurus* since response intensity, but not initiation, was suppressed. Both *Panulirus* and *Podochela* typically move long distances while grazing. Their assessments of prey quality and density are likely to occur on the patch-level of resource organization, where a "stop and feed" rule is most advantageous. *Pagurus*, on the other hand, is a microphagous detritivore that is active yet limited in mobility due to its small size. Given the limitations in the patch-selection ability of *Pagurus*, variable ingestion rates may be the most important animal response affecting feeding energetics. An optimal foraging model predicts that the net time rate of energy gain is maximized when benthic deposit- and suspension-feeders covary ingestion rates positively with food value (Taghon, 1981). This is because such animals are unable to sample their environments and hence to choose among food items to the same degree that highly mobile predators
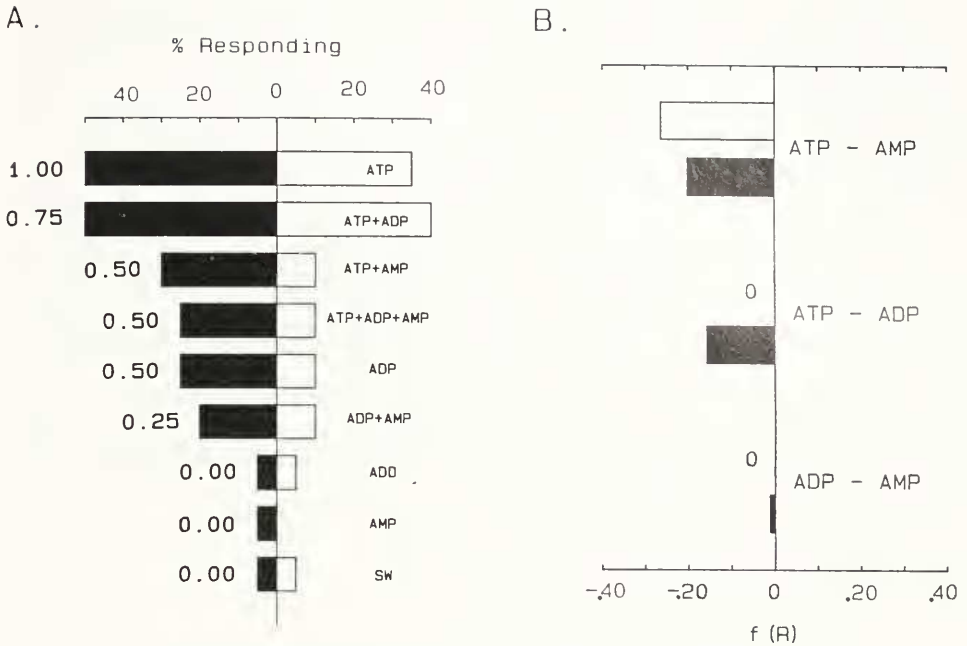
FIGURE 7.   A. Feeding and locomotory responses by lobsters to single adenylates and mixtures. Values for adenylate energy charge appear (0–1 scale). B. Independent component indices for binary interactions between phosphoadenylates. Each chemical was presented at 10^{-2} M. Open bar (□), feeding; closed bar (■), walking.

can. Benthic marine organisms lacking mobility are dependent on food being brought to them by water currents, by lateral and vertical advections (Taghon *et al.,* 1980), and by microbial regeneration within sediments (Levinton and Lopez 1977; Newell, 1979).

By responding to ATP, *Panulirus* is similar to many of the haematophagous insects. Among Diptera, three species of culicine mosquitoes, the blackfly *Simulium venustum* (Smith and Friend, 1982), the tsetse fly *Glossina austeni* (Galun and Margalit, 1969), and the horsefly *Tabanus nigrovittatus* (Friend and Stoffolano, 1983) all require ATP or ADP as a phagostimulant. Responses by insects are thought to be adapted to the release of phosphoadenylates, particularly of ATP and ADP, associated with recruitment of blood platelets to open wounds. Apparent sensitivity by *Panulirus* to adenylate energy charge [AEC = (ATP + 0.5 ADP)/(ATP + ADP + AMP)] could enable it to assess the total metabolic energy available to a prey (Atkinson, 1977). Chemical excitation of lobsters was ATP > ADP > AMP = adenosine, which is the pathway followed by phosphoadenylates in autolytic degradation of animal flesh (Hiltz and Dyer, 1970). Dephosphorylation of ATP proceeds rapidly during cell death; also, stress related to disease, injury, and starvation elicit physiological defense responses (Selye, 1976) that increase metabolic activity and ATP use (Chapman *et al.,* 1971; Balch 1972; Walker-Simmons and Atkinson 1977; Ostolovskii 1978; Buikema *et al.,* 1979).

Optimal foraging theory usually predicts that grazers should become more selective at high food densities and less selective at low food densities (Pulliam, 1974; Pyke *et al.,* 1977; Owen-Smith and Novellie, 1982; Pyke, 1984). A corollary is that food
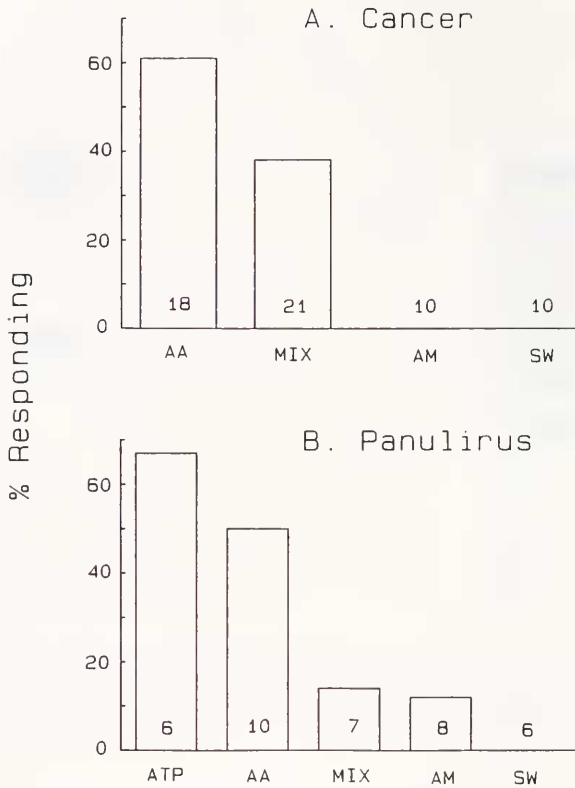
FIGURE 8.   Responses to ATP, glycine (AA), ammonia (AM), glycine + ammonia (MIX), and seawater (SW), by (A) crabs and (B) lobsters. Animals were placed in large tanks, and each chemical was presented at 10^{-5} M. The number of animals tested is shown.

selectivity should decrease with increasing food deprivation and starvation, if recognition or assessment of food availability is modified by hunger levels (Snyderman, 1983). When grazers approach satiation they should behave as if food were abundant and become more selective (Schoener, 1971; Pulliam, 1974; Charnov, 1976). In this study, animals were maintained near satiety and they were without risk of death due to starvation. Therefore, chemical preferences might be expected for odors that signify food of highest energy and nutrient payoffs. Optimal foraging theory predicts that feeding responses should become more broadly tuned as food deprivation increases (or as prey densities are lowered), and as energy reserves are spent. That is, we should expect mixture suppression by ammonia and AMP to decrease as food becomes limiting. Mixtures should become more attractive at lower adenylate energy charges and at lower amino acid:ammonia ratios. These predictions have yet to be tested.

Caution is urged in developing hypotheses of "optimal" chemoreception. Many factors operate that could confuse experimental design and render test results meaningless. For example, optimality only can be tested fairly under the constraint that animals behave *given* their sensory, motor, and CNS capabilities. It is AMP rather than ATP that acts as a potent chemoattractant to the grass shrimp, *Palaemonetes pugio* (Carr and Thompson, 1983). Because this animal principally scavenges dead

animal and detrital materials (Walsh, 1975), the AMP response may be adapted to the dietary mode and need not exclude an optimal chemoreception hypothesis. Differences in adenylate responses by *P. interruptus* and *P. pugio* correlate precisely with differences in the electrophysiological response patterns by "ATP-best" and "AMP-best" olfactory receptors in the Florida spiny lobster, *Panulirus argus* (Derby *et al.,* 1984; Carr *et al.,* 1986). The identification of receptor types with response spectra that can account for observed behavior provides a mechanistic argument required to augment theoretical ecological considerations.

Ammonia is chemoattractive under some conditions, though this ability depends on the capacity of an organism to assimilate ammonia-nitrogen, or to use ammonia as a cue specific to preferred food. Motile phototropic algae, *Chlamydomonas* (Sjoblad and Frederiksen, 1981), *Dunaliella* (Sjoblad *et al.,* 1978), and *Symbiodinium* (Fitt, 1985), all exhibit positive chemotaxis to ammonia gradients. These organisms use ammonia as preferred substrate for inorganic nitrogen during protein synthesis. Scavenging animals and detritivores also may be found attracted to ammonia. They typically depend on biodegradatory bacteria as a principal source of carbon and nitrogen (Newell, 1965; Fenchel, 1970; Hargrave, 1970; Lopez *et al.,* 1977; Wetzel, 1977). Previous investigators have argued that because ammonia is excreted by all living marine heterotrophs, it might signal the presence of nearby prey (Borroni *et al.,* 1986). However, such a cue would not allow for prey discrimination, for differentiation between predator and prey, or for distinction between living prey and aged carrion. The amino acid to ammonia ratio, on the other hand, provides a continuum on which living and dead prey can both be scaled.

Foragers frequently base their preferences on distinguishing prey taxonomic differences. Evidence shows that odor and taste discriminations often depend on unique blendings of chemical substances (Dethier, 1974; Atema *et al.,* 1980). Feeding suppression may therefore arise as a consequence of mixtures that specify inappropriate prey images, independently of the perceived energy and nutrient properties. This may explain why investigators sometimes find suppressant interactions among amino acids (McLeese, 1970; Allison and Dorsett, 1977; Johnson and Atema, 1986). Sensory mechanisms evolve to economize resource use. It should be possible to combine ecological, evolutionary, and physiological arguments to construct testable hypotheses that predict psychophysical events which influence the chemical perception of food.

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